ON A CASE OF FACULTATIVE PARTHENOGENESIS IN THE GYPSY–MOTH LYMANTRIA DISPAR L. WITH A DISCUSSION OF THE RELATION OF PARTHENO-GENESIS TO SEX

RICHARD GOLDSCHMIDT,

KAISER-WILHELM INSTITUT FÜR BIOLOGIE, BERLIN.

In the discussion about the relation of parthenogenesis and sex, revived after the discovery of the sex-chromosomes, cases of facultative parthenogenesis in normally bisexual animals play a rather doubtful part. As the great majority of such reports belongs to the older and oldest literature, modern writers appear sceptical in regard to their reliability. Therefore any new case recorded under reliable conditions must command the attention of biologists.

The majority of the reports about facultative parthenogenesis relate to the order Lepidoptera. In most cases only the hatching of caterpillars from unfertilized eggs has been observed, which is of no interest for us here. There are comparatively few cases where adults have been raised and their sex stated. One set of observations relates to the silk-moth. This case can be regarded as settled. There can be no doubt to-day that there are races of the silk-moth which exhibit regularly the phenomenon of facultative parthenogenesis and that the normal number of both sexes is produced from parthenogenetic eggs (for example, see Hartmann, '12). Another set of facts relates to the Psychidæ, where parthenogenesis is a normal phenomenon, resulting in female offspring. A third series of reports deals with occasional cases of parthenogenesis in the gypsy-moth, *Lymantria dispar* L. In 1870, H. Weijhenberg, Jr., reported that he had succeeded in breeding 27 adults, 14 ♀ and 13 ♂, from 60 virgin females of this moth. He also obtained a second parthenogenetic brood, but he does not give details (see Dohrn, '71). A second report comes from G. Platner ('88). He claims to have obtained parthenogenetic eggs regularly by keeping the females isolated for a

35

prolonged period. He states, furthermore, that the maturation-divisions in these eggs are normal. However, a full report of this work never appeared. Since that time many investigators have tried to get parthenogenetic offspring from the gypsy-moth, always in vain. I know that many of those who worked experimentally with the gypsy-moth have tried it again and again, without any success. We and some of our students have used most of our odd material in females for this purpose during the last seven years. The complete failure in every case made us, as well as other observers, believe that the old reports must be based on experimental errors. Nevertheless they seem to be true, for I finally, in 1915, succeeded in getting a parthenogenetic egg-batch.

In this case the conditions of the experiment excluded the possibility of error. I had isolated, for a selection experiment, 4 caterpillars, which were kept in a fruit-jar with a tightly screwed tin cover. After pupation three pupæ died from polyhedra disease. The fourth, a female, hatched. As the experiment was spoiled I left this individual in the closed jar, intending to kill it later. When I opened the jar after a few days the female was busy laying a regular normal egg-sponge, which is normally never done by unimpregnated females. From this parthenogenetic egg-batch, containing certainly over 200 eggs, 22 caterpillars hatched in the spring 1916 and were bred with special care. Three died in early stages and the sex could not be ascertained. Three died before pupation. They were females. Three were killed between the third and fourth moult for cytological study, and proved to be one female and two males. The remaining thirteen hatched and were three females and ten males, the total thus being seven females, twelve males and three unknown. The three females were tried again for parthenogenesis and one of them after ten days finally laid a normal-looking egg-batch. There can, therefore, be no more doubt that facultative parthenogenesis occasionally occurs in the gypsy-moth and results in the production of both sexes. We do not, however, know whether favorable external conditions or some hereditary or not hereditary quality is responsible for the occurrence. The parthenogenetic mother was, in our case, an

F_1-hybrid between a European and a northern Japanese race of gypsy. But neither the parental races nor the other F_1 and F_2 individuals produced parthenogenetic eggs, although ample opportunity was given to many isolated females. This fact neither excludes nor favors the possibility of parthenogenetic strains or mutations.

In order to give an interpretation of these facts it is very important to know the behavior of the chromosomes of these parthenogenetic eggs. A study of the maturation divisions was, of course, impossible. But we were able to ascertain that ovogonia, as well as spermatogonia, of the parthenogenetic caterpillars contained the normal (diploid) number of chromosomes. A visible difference between the chromosome-sets of the two sexes does not, however, exist in the gypsy-moth. The literature on parthenogenesis contains, so far as we are aware, only two statements which relate to our case. One is Platner's already quoted paper, where he states that the reduction-divisions in parthenogenetic dispar-eggs are normal. However, he does not mention the chromosome numbers and we do not know whether the eggs studied by him would have developed. Henking ('92) studied the reduction-divisions of parthenogenetic silk-worm eggs and found a normal reduction-division. But his eggs never developed embryos; therefore his results are of no value for us.

For a real understanding of the relation of parthenogenesis to sex it is very important to know how the diploid number in other parthenogenetic animals is formed. If we compare our case with others where the cytology of parthenogenesis has been worked out, we immediately realize that there are different possibilities. In the first place, parthenogenesis could occur without a reduction-division, as seen in aphids and other forms. Or parthenogenesis could be started after a reduction-division by secondary fusion of the egg-nucleus and the reduction-nucleus, as has been shown for *Artemia* and the starfish. Or, thirdly, an apparently normal formation of the polar bodies could occur, but without reduction of the chromosomes, caused by their failure to conjugate, as has been shown for *Nematus* (Doncaster, 1906) and *Rhodites* (Schleip, 1909). Finally, it is possible that, after normal reduction-divisions, the diploid number is restored before

segmentation by a rudimentary division. No case of this kind has been proved beyond doubt.

The current ideas about the relation of parthenogenesis and sex are primarily concerned with the chromosome number and with an eventual extrusion of a single sex-chromosome. If these conceptions are valid, the different methods of reaching the diploid number of chromosomes would not affect the resulting sex. But, at the same time, these conceptions have failed to explain why parthenogenesis produces only males or only females or both sexes, and that sometimes with, sometimes without, reduction. The ideas about sex-determination which we have developed during the last few years enable us, as we believe, better to understand the different facts about parthenogenesis and to fit them into the general scheme of sex-inheritance.

Since we stated our views in a general way not long ago (Goldschmidt, 1916), we do not need to repeat them here in extenso. We might mention only that we believe to have proved (1) that there are different sex-factors for the sexes, both acting independently in both sexes; (2) that both factors exhibit a definite quantitative action; (3) that the definitive sex depends upon which factor has the higher value, or, expressed in a formula, $F - M > e = ♀$, $M - F > e = ♂$; (4) that one of these factors is carried in the sex-chromosome, the mechanism of their distribution—or, in Mendelian symbolism, of the gamete-formation in heterozygosis—being the means of regulating the values for e in favor of F or M respectively; (5) that the factor not carried in the sex-chromosome, namely F in the case of female heterozygosis, M in male heterozygosis, is inherited maternally, probably in the protoplasm of the egg.

Thus the conclusions which we must draw concerning the relation of parthenogenesis and sex are of course different from those of older writers. Let us first glance at the possible combinations to be derived from our conceptions. For convenience we use the formulæ: $(FF)\ Mm = ♀$; $(FF)\ MM = ♂$, in the case of female heterozygosis, and $(MM)\ Ff = ♂$, $(MM)\ FF = ♀$, in the case of male heterozygosis. And we keep in mind the fact that the factors within the brackets are inherited maternally and are, therefore, contained in every egg, the others being carried

by the x-chromosomes and following their distribution. The
possibilities are now as follows:

1. Female heterozygosis.   ♀ = (FF) Mm, ♂ = (FF) MM.

    A. Parthenogenesis occurs with the reduced number of
chromosomes. Offspring must be female as no set MM
can be produced.

    B. Parthenogenesis occurs with normal number of chro-
mosomes in consequence of no reduction-division taking
place. All offspring are female, as the maternal com-
bination is preserved.

    C. Parthenogenesis occurs with the normal number of
chromosomes, reached by readjustment after reduction.

        a. Readjustment accomplished by conjugation of egg
and polar nucleus. All offspring female, since
maternal combination remains.

        b. Readjustment accomplished through rudimentary
division before cleavage. The reduction had led to
eggs with M and eggs with m. M eggs then become
MM, *i. e.*, males, m eggs become mm, *i. e.*, females,
if viable at all.

Conclusion.—Parthenogenesis with female heterozygosis can
result in the production of (*a*) females exclusively (cases *A*, *B*,
Ca); (*b*) males exclusively (case *Cb* when mm eggs not viable);
(*c*) both sexes (case *Cb* if all eggs are viable, or any combination
of *Cb* with the other cases).

2. Male heterozygosis. (MM) FF = ♀ ; (MM) Ff = ♂.

    A. Parthenogenesis occurs with the reduced number of
chromosomes. Offspring nothing but males. However,
the occasional formation of females is possible when a
case of non-disjunction occurs, leaving both FF inside
the egg.

    B. Parthenogenesis occurs with the normal number of chro-
mosomes in consequence of the failure of reduction. The
maternal combination being preserved, all offspring are
female. In this instance males can be produced if one
x-chromosome is extruded during the equation division.

    C. Parthenogenesis occurs with the normal number of chro-
mosomes reached by readjustment after reduction.

> a. Readjustment through conjugation of egg and polar nucleus. The maternal combination being preserved, only females are produced.
>
> b. Readjustment through rudimentary division before cleavage. Only female offspring result, since every egg contains FF. In case of non-disjunction, an exceptional male may appear, provided an ff egg is viable.

Conclusion.—Parthenogenesis with male heterozygosis can result in the production of (a) females exclusively (cases B, C), exceptional males explained by Cb or the occasional occurrence of A or B; (b) males exclusively (case A), exceptional females explained by non-disjunction or the occasional occurrence of B, C; (c) both sexes (case B or combination of A with B or C).

We may now, by surveying briefly the facts known about parthenogenesis, show that the above explanation holds good for all of them.

1. *Hymenoptera.*—The classic case of the bee is of special interest because it demonstrates the possibility of sex-differentiation without the use of the usual method of the formation of two kinds of gametes. It is important also because it shows that we are entirely at a loss if we express ourselves in Mendelian symbols without referring to the cytological facts. Parthenogenetic eggs produce males which develop with the reduced number of chromosomes.[1] We are concerned with case $2A$ of the series above described. In spermatogenesis no reduction occurs and only one kind of spermatozoa is formed, being in constitution identical with the ripe egg. Every fertilized egg, therefore, develops into a female. Occasional females derived from parthenogenetic eggs—reported from time to time—(the same for ants)—can be explained by non-disjunction ($2A$) or the occasional occurrence of $2B$, C. Occasional males from fer- fertilized eggs are also possible if a non-disjunction egg (with both FF in the polar body) is fertilized.

The other hymenoptera show no difference in principle. Where parthenogenesis results in the formation of both males and females, the former develop with the haploid number of chro-

[1] For cytological facts see Nachtsheim, H. ('13).

mosomes (case 2*A*), the latter with the diploid number (2*B*). Spermatogenesis and fertilization are the same as in the bee (*Neuroterus* according to Doncaster, '10).   If parthenogenesis results in female offspring, development occurs with the diploid number, no reduction taking place in spite of two maturation divisions (*Nematus*, Doncaster, '09, *Rhodites*, Schleip, '09).   Occasional males as in 2*A* or 2*Cb*.

2. *Rotatoria.*—The relation of parthenogenesis to sex seems to be exactly the same as it is in Hymenoptera.   (Lauterborn, '98, Shull, '10, Whitney, '09).   Parthenogenetic eggs without reduction give females, with reduction males, the latter if fertilized, females.   We must suppose that the spermatogenesis is similar to that of the bee.

3. *Aphids.*—The well-known work of Morgan ('09) and von Baehr ('09) shows them to fall into case *B*.

4. *Phasmids.*—Their behavior is not yet clear, either experimentally or cytologically.   Probably they behave like some gall-wasps with occasional males (see von Baehr, '07).

5. *Lepidoptera.*—The group of the Psychidæ, which exhibits regular parthenogenesis, is cytologically most interesting, as will be shown in a paper by Dr. Seiler now in press.   The results seem to fit our conceptions.   About the cases of facultative parthenogenesis as described here we know only that both sexes are produced and contain the diploid number of chromosomes. We must suppose that we are concerned with case 1*Cb* or 1*Cb* combined with 1*B* or 1*Ca*.

6. *Ostracoda and Cladocera.*—Although these groups are greatly favored by experimentalists, we know comparatively little about their cytology (Woltereck, '98, Schleip, '09, Kuehn, '08). It is possible that they belong to the same group as the Rotatoria, but in *Ostracoda* parthenogenetic female-producing eggs undergo no reduction division.   The experimental results in sex-production in this group make it seem possible, however, that we are here concerned with something quite different.   This possibility will be discussed on another occasion.

7. *Artemia.*—The most recent writers on the subject (Artom, '11, Fries, '09) agree that the parthenogenetic races develop with the diploid number of chromosomes, the bisexual races in

the usual way. Nothing is known about the cytology of the occasional males in the parthenogenetic races. It is therefore impossible to tell with which of the possibilities we are here dealing.

8. *Nematodes.*—The strange type of parthenogenesis described for a Rhabditis by Krueger ('12) and resulting in female off-spring, occurs without a reduction of the chromosomes. Here we have case 2B.

9. *Echinoderms.*—(Artificial parthenogenesis.) Tennant's work makes it pretty certain that the male is heterozygous. Artificial parthenogenesis with reduced chromosome number ought to yield males as in the bee. This has been found to occur in the few recorded specimens.

10. *Amphibia.*—(Artificial parthenogenesis.) We do not know which sex is heterozygous in Amphibia. R. Hertwig thinks it is the male. We tried ('11, '13) to show that the experimental results favor the view of female heterozygosis. Moreover we do not know whether parthenogenesis takes place with the haploid or the diploid number of chromosomes. The expectations can therefore fit any of the above enumerated cases.

I want to emphasize, finally, the fact that our thesis, if expressed in terms of cytology, is nothing but Wilson's old hypothesis of the one portion-two portion *x*-substance. But our experiments have allowed us to give a physiological meaning to this conception and to bring this cytological conception into harmony with Mendelian formulations.

OSBORNE ZÖOLOGICAL LABORATORY,
   YALE UNIVERSITY, NEW HAVEN, CONN.

LITERATURE.

Artom, C.
   '11 Analise Comparativa della sostanza cromatica, etc. Arch. Zellforsch., 7, 1911.

Baehr, W. B. von
   '07 Ueber die Zahl der Richtungskoerper in parthenogenetisch sich entwickeln-den Eiern von Bacillus rossii. Zool. Jahrb. (An.), v. 24.

   '09 Die Oogenese bei einigen viviparen Aphididen, etc. Arch. f. Zellforsch., v. 3.

Dohrn, C. A.
   '71 Aus Parthenogonien. Entomol. Ztg. Stettin, 32.

Doncaster, L.
   '06 On the Maturation of the Unfertilized Egg and the Fate of the Polar Bodies in Tenthredinidæ. Qu. J. Micr. Sc., 49.

'10 Gametogenesis of the Gall-Fly, *Neuroterus lenticularis*. Proc. R. Sc. B., 82 and 83.

Goldschmidt, R.

'11 Erblichkeitsstudien an Schmetterlingen. I. Zeitschr. ind. Abst., 7.

'13 Einführung in die Vererbungswissenschaft. 2. Aufl., 1913.

'16 Experimental Intersexuality and the Sex-Problem. Amer. Natur., v. 50.

Hartmann, M.

'12 Vererbungsstudien. I. Zool. Jahrb. Suppl., 15, v. 3.

Henking, H.

'92 Untersuchungen, etc. Zeitschr. wiss. Zool., 54.

Hertwig, R.

'12 Ueber den derzeitigen Stand des Sexualitaetsproblems. Biol. Centrbl., 32.

Krueger, E.

'12 Die phylogenetische Entwickelung der Keimzellenbildung einer freilebenden Rhabditis. Zool. Anz., 40.

Kuehn, A.

'08 Die Entwickelung der Keimzellen in den parthenogenetischen Generationen der Cladoceren, etc. Arch. f. Zellforsch., 1.

Lauterborn, R.

'98 Ueber die cyclische Fortpflanzungsweise limnetischer Rotatorien. Biol. Centrbl., 18.

Morgan, Th. H.

'09 A Biological and Cytological Study, etc. Journ. Exp. Zool., 7.

Nachtsheim, H.

'13 Cytologische Studien ueber die Geschlechtsbestimmung bei der Honig-biene. Arch. f. Zellforsch., 11.

Platner, G.

'88 Die erste Entwickelung befruchteter und parthenogenetischer Eier von Liparis dispar. Biol. Centrbl., 8.

Schleip, W.

'09 Die Reifung des Eis von Rhoditis rosae, etc. Zool. Anz., 35.

'09 Vergleichende Untersuchung der Eireifung bei parthenogenetischen und be geschlechtlich sich fortpflanzenden Ostracoden. Arch. f. Zellforsch., 2.

Shull, A. F.

'10 Studies in the Life Cycle of Hydatina senta. I. Journ. Exp. Zool., 8.

Tennant, D. H.

'12 The Behavior of the Chromosomes in Cross-fertilized Echinoderm Eggs Journ. Morph., 23.